

ON *TIVELA* AND *GRATELOUPIA*.

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As the dentition of these shells presents exceptional features and as I find that erroneous views regarding the structure of their hinges are largely eurrent, a note on the subject, with the special object of fixing the taxonomical rank of the fossils known as *Grateloupia* and *Cytheriopsis*, seems to be required.

With respect to *Tivela*, no one seems to have fully and correctly described the positions of the cardinal teeth, nor their complete separation from the accessory dentiform ridges or rugosities. Most writers, indeed, such as S. P. Woodward, Deshayes, Adams, and Dall, have regarded all these dentiform ridges as cardinal teeth, and have stated that the teeth vary in number from 3 to 7 in each valve. Others, like Fischer and Cossmann, seem to have mistaken the first supplementary tooth or ridge for the normal posterior cardinal, and to have overlooked the small and slender anterior cardinal of the right valve.

Having examined the dentition of many species of *Tivela*, both in young and adult specimens, and having compared it with that of *Meretrix* and *Sunetta*, which are the most nearly allied genera, I can state with confidence that the *three* normal cardinal teeth of those genera are present in all species of *Tivela*, although their position varies, because they are more or less displaced by the growth of the supplementary teeth or ridges. This displacement is often carried to such a degree that the three real cardinal teeth are crowded into the anterior half of the hinge-plate, while the accessory teeth occupy the expanded posterior half.

These accessory teeth do not appear to be survivals of primitive embryonic ridges, for they are often less definitely developed in young shells than in adult specimens, and an examination of their number and position in many different species has convinced me that they are developed out of the original nymphal rugosities by the formation of parallel grooves and ridges on this plate.

1. *TIVELA*.

The simplest form of hinge in *Tivela* is exemplified in that of *T. ponderosa*, Koch. In the right valve of this species the three ordinary divergent teeth of the Meretricine group are easily distinguishable, the anterior tooth being very narrow and slender and close to the lunular border, the median thick, solid, and triangular, and the posterior narrow and grooved at the top. Beyond this and below the ligament the nymphal plate is thickened and rugosely striated, but is not raised into any tooth-like projections. In the left valve the teeth are widely divergent and the posterior cardinal occupies its normal position, but its upper and outer side is rugose, as also is the nymph above it.

A distinctive character of the *Tivela* hinge is the forward position of the anterior cardinals in both valves, that of the left being in line with the long compressed anterior lateral, so that these two teeth have the appearance of being projections from one long continuous ridge; that of the right valve is always placed so close to the anterior margin and is moreover so low and slender that it may easily be overlooked, and in some species it does become obsolete in adult shells, though it is always discernible in young specimens.

In most species of *Tivela* the pallial sinus is short and small, but in *T. ponderosa* it is deep and wide, reaching horizontally about half-way across the shell and impinging on the pallial line below. The size and depth of the sinus vary much in different species, and it should not be described as always small.

T. damaoides, Gray, from Peru, has the same hinge-characters as *T. ponderosa*, and the specific differences are so small that it may be regarded as a mere variety of the latter. In the right valve of *damaoides*, however, the inner edge of the nymph is raised into a narrow tooth-like ridge (Fig. 1).

T. bicolor, Gray, from West Africa, has a similar hinge, the nymph of the right valve being nearly flat and only slightly rugose; so also are those of *T. tripla* (Linn.) and *T. dolabella* (Sow.); *T. polita* (Sow.) has a similar flat rugose nymph, and is remarkable for its deep pallial sinus, which extends more than half across the shell and obliterates part of the pallial line.

In *T. stultorum* (Mawe), which is better known as the *T. crassatelloides* of Conrad, there is a further development of this ridge, the whole thickness of the nymph in the right valve being produced or raised into a rugose dentiform ridge which forms a supplementary tooth, but is clearly only a thickened development of the nymph. This fits into a rugose trough or space between the posterior cardinal of the left valve and a narrow ridge or plate on the nymph above it.

T. natalensis (Dunker) is interesting because it shows what seems to be the first stage in the development of two nymphal teeth. The nymph is not thickened as in *crassatelloides*, being still low and flattish, but is grooved or channelled along the median line, and the left valve carries a narrow tooth-like ridge which fits into this groove. The hinge thus presents the appearance of having four cardinal teeth in each valve, for the grooved nymph might be mistaken for a bifid posterior tooth.

In this species also it is noticeable that there is a rather wider space between the nymph of the right valve and the true posterior cardinal, so that the latter is shorter and more central in position than is the corresponding tooth in the species previously mentioned; it is a straight, narrow, entire tooth, very different from the elongate grooved or bifid posterior of *Meretrix*, and it is united at the top, under the umbo, to the end of the lunular margin of the shell, as in *Meretrix* and other genera of Veneridæ.

In *T. compressa* (Sowerby) the nymphal plate is broader, and there are several parallel rugosities, the inner one of which becomes in

old shells a rough irregular ridge. This inner ridge is still more prominent in *T. nitidula* (Sow., non Lam.).

T. intermedia (Sow.) furnishes a good example of the next stage in the development of accessory teeth, for in this species the nymph is much thickened and divided into two parts by a deep central groove, so that there are two distinct dentiform ridges. Moreover, the three

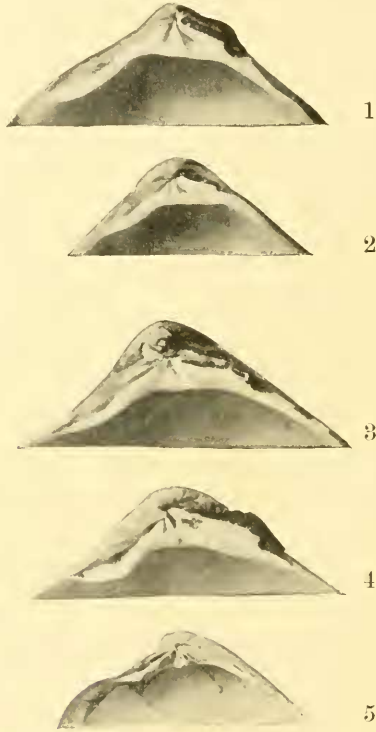


FIG. 1. *Tivela damaoides*, Gray.
 ,, 2. ,, *mactroides* (Born).
 ,, 3. ,, *argentina* (Sow.).
 ,, 4. ,, *gracilior* (Sow.).
 ,, 5. *Grateloupia irregularis*, Bast.

normal teeth are crowded into the anterior half of the cardinal plate; the anterior cardinal, though visible in young specimens, becomes obsolete with age, the median is narrowly triangular and directed forward, while the posterior is very narrow, short, straight, and almost vertically central.

In the left valve the posterior cardinal is also central, rather thick, and bifid when young; the nymphal area beyond it is thickened,

very rugose, and roughly divided into two ridges by a longitudinal groove.

In *T. planulata* (Brod. & Sow.) and in *T. hians* (Phil.) the nymphal plate is very deep, and there are two ridges on the inner side of it in the right valve and two smaller ones on the left valve.

T. nubila (Gray), *T. mactroides* (Born), *T. trigonella*, and *T. laevigata* (Gray) have hinges like that of *T. intermedia*. In *mactroides* the rugose area of the right valve (Fig. 2) has a deep central groove and a second shallow one under the base of the ligament, so that there is an appearance of three parallel teeth. In the left valve there are two narrow ridges corresponding with these grooves, and the posterior cardinal is only united to the nymph at the top.

In *T. radiata* (Sow.) and *T. gracilior* (Sow.) we seem to have the ultimate phase of this line of development, for in these species, which are quite distinct from one another, the cardinal plate has the appearance of carrying six cardinal teeth. In *T. radiata* (right valve) the true posterior cardinal is actually nearer the anterior than the posterior end of the plate, while the first accessory tooth is a well-developed dentiform ridge separated from the next by a deep groove, except at the top, where it merges into the nymph; the second is also a long narrow ridge, and the third a shorter and less elevated one. The anterior cardinal is small but visible just inside a bulge of the lunular margin. In the left valve there are two well-developed accessory tooth-ridges behind the normal posterior cardinal, which is separated from them by a deep groove.

In *T. gracilior* the dentition is similar, but there is a wider space between the normal and the supplementary teeth of the right valve, so that the different origin of the two sets of teeth is very clearly seen. The interspace extends right up to the umbo, the posterior cardinal is united to the lunular margin, while the accessory teeth are obviously ridges on the nymphal plate, produced simply by the grooving or channelling of that plate. The hinge-plate is thus clearly divided into two parts, and there is a complete break or discontinuity between the anterior margin of the shell and the nymph or ligamental plate. In the left valve, however, this separation is not quite so complete, because the posterior cardinal of that valve is attached to the top of the nymph, springing, in fact, from the posterior and not from the anterior margin.

Finally, in *T. argentina* (Sow.) we have a rather different development, for in this species the nymph is not grooved longitudinally, but obliquely, and only on a portion of its surface (Fig. 3). Its anterior part is sculptured into four or five short oblique ridges, which are roughly but not very regularly parallel to one another, while the posterior part of the area is smooth. These oblique ridges, though less like teeth than the strongly developed ridges of *T. gracilior* (Fig. 4), are really more like those of *Grateloupia* than is the case in any other species of *Tivela*. All three of the normal teeth are clearly developed, and the right posterior is strongly united to the end of the anterior margin, but the left posterior is adherent to the thickened nymph of that valve.

2. GRATELOUPIA.

This name was given by Desmoulins to certain shells of Miocene age which occur near Bordeaux in France, in Italy, and in Austria, but only two species have been described. The typical form is the *Donax irregularis* of Basterot (1825), which was more completely described and well figured by Desmoulins in 1828¹ as the type of a new genus, to which he gave the name of *Grateloupia*. The following is that part of his description which relates to the hinge: "Dentes cardinales primarii (ut in *Cytherea*) divaricati, tres in utraque valva; quibus accedunt in valvis ambabus dentes cardini-seriales 3-6 lamellosi, paralleli, ad natem convergentes oblique rugosi, margineque denticulati, sub ligamento ad latus testæ posticum instructi. Dens lateralis unicus, anticus, sub ano (ut in *Cytherea*) in valva sinistra positus; fovea in valvâ dextrâ alterius valvæ dentem lateralem recipiente."

From this account (which is given also in French) it is quite clear that Desmoulins thoroughly understood the structure of the hinge, for he rightly credits it with three principal or primary teeth and several parallel accessory teeth, placed obliquely under the ligament, which he terms '*cardini-seriales*', not *cardinales*.

It is curious that although he was fully aware of the existence of a similar shell in the Miocene deposits of Bordeaux, namely the *Donax difficilis* of Basterot, yet he and Deshayes regarded this as belonging to *Cytherea*. Possibly this may have been due to his not possessing sufficiently good specimens, for the dentition is really the same, though the number of accessory ridges or teeth is less—only two or three in a more contracted space. It was, however, recognized as a *Grateloupia* by C. Mayer in 1858.²

Deshayes accepted the genus in 1848 (*Traité Élémentaire de Conchyliologie*), but S. P. Woodward considered it to be only of subgeneric rank; in the first edition of his *Manual* (1851) he placed it as a sub-genus of *Cytherea*, and in subsequent editions as a sub-genus of *Trigona*, which is the *Tivela* of Link. Most subsequent authors, d'Orbigny (1852), Sowerby (1852), Bronn (1854), Pietet (1855), and Hoernes (1862), accepted it as a genus; while Fischer, in his *Manuel de Conchyliologie* of 1887, not only described it as a genus, but separated it entirely from *Tivela*, which he placed as a sub-genus of *Meretrix*.

It seems to have been Fischer who first imagined that a posterior lateral tooth existed in the right valve of *Grateloupia*. He correctly stated that there are "trois dents cardinales divergentes" in each valve, and "plusieurs plis dentiformes, parallèles, placés en arrière de la dent cardinale postérieure", but he adds that there are two anterior lateral teeth and one posterior lateral in the right valve. No doubt this was the chief reason why he separated *Grateloupia* from *Tivela*.

His opinion has naturally influenced other French writers, and it has recently been adopted by Messrs. Cossmann & Peyrot,³ who

¹ Actes Soc. Lin. Bordeaux, ii, p. 243, pl. vi, figs. 1-5.

² Journ. de Conch., tom. vii, p. 88, 1858.

³ "Conch. Neogen de l'Aquitaine": Actes de la Soc. Linn., Bordeaux tom. lxxiii, 1909.

not only mention the existence of this supposed posterior lateral as a generic character, but show its position in their diagram of the hinge of *G. irregularis*. In their description of this species, however, they write of it as "très rudimentaire, la fossette opposée étant très indecisée", while under *G. difficilis* they remark that there is "pas d'apparence de lamelles postérieures, le bord supérieur est seulement un peu rainuré".

Thus these authors admit that the supposed posterior lateral does not exist in *G. difficilis*, and that it is very rudimentary in *G. irregularis*; hence it is impossible to regard it as a generic feature. Having examined good specimens of both species, which I owe to the kindness of Professor Peyrot, I can quite confirm their statements; I am not surprised that they regard the tooth as very rudimentary, even in *G. irregularis* (Fig. 5), for I feel sure that it has no real existence. The feature which has given rise to the idea of such a tooth is a slight inflection of the posterior margin of the valve beyond the end of the ligament, and a thickening of the inner border of the groove which exists in all species of *Tivela* and *Meretrix*. The extent of this thickening varies with the individual and with the age of the shell, and it has been exaggerated in some figures of the shell, notably in that given by Hoernes (op. cit., pl. xvi, fig. 56). Moreover, no one has claimed to recognize a corresponding tooth on the posterior border of the left valve; no elevation exists on that border, and its absence militates strongly against the existence of a lateral tooth in the right valve.

As, however, I did not wish to dissent from such authorities as Messrs. Fischer, Cossmann, and Peyrot without confirmation of my opinion, I sought that of Messrs. E. A. Smith and R. B. Newton, of the British Museum, who have kindly examined the specimens of *G. irregularis* in the National Collection, and have informed me that they agree in considering that "there is no posterior lateral tooth in *Grateloupia*".

This being so, there is really no essential generic difference between *Grateloupia* and *Tivela*; indeed, the differences are scarcely of sub-generic importance. The dentition of *Grateloupia* is similar to that of *Tivela argentina*, *T. radiata*, and *T. gracilior*. The two parts of the hinge-plate in the right valve are similarly separated by a deep groove or space, in front of which are three divergent cardinal teeth, while behind it are a set of oblique and parallel plaits or ridges, varying in number from three to ten. The true posterior cardinal is a straight, narrow tooth, placed vertically under the umbo, and connected at the top with the anterior margin of the valve. In some specimens it is, moreover, visibly bifid or grooved.

The pallial sinus in *G. irregularis* is large, deep, linguiform, and horizontal, extending to within a short distance of the anterior adductor scar, but in *G. difficilis* it is smaller and shorter, not reaching much more than half-way across the interior space. We have already seen (p. 267) that the depth of the sinus varies also much in *Tivela*, and it is certain that the form of the sinus cannot be taken as a character of generic or subgeneric importance.

There is nothing, in fact, about these two species of shells to mark them off as more than a section of *Tivela*, and they are actually associated with a third species which Messrs. Cossmann and Peyrot rightly regard as a typical *Tivela*; this is *T. triangularis* (Bast.), which closely resembles the recent *T. dolabella*. Messrs. Cossmann and Peyrot have retained *Grateloupia* as a genus, and have placed *Tivela* under it as a sub-genus, but this is contrary to the rule of generic priority, for Link's genus was proposed in 1807 and Desmoulin's in 1828, so that the proper arrangement is to make *Grateloupia* a section or sub-genus of *Tivela*.

CYTHERIOPSIS (Conrad).

This supposed genus or sub-genus was founded on a fossil from the Eocene of Alabama (United States), but it is probably only a form of *Grateloupia*, and consequently of *Tivela*, for the distinction which Dr. Dall makes between them is a mistake, arising apparently from a miscomprehension of the dentition. He states that in *Grateloupia* "the posterior right cardinal is fused with the nymphal rugosities", and that in *Cytheriopsis* it is the left posterior cardinal which is so fused. As regards *Grateloupia* this statement is absolutely incorrect, for there is a deep space in the right valve between this tooth and the nymphal plate.

With respect to *Cytheriopsis*, which is the *Cytherea hydana* of Conrad (August, 1833) and the *Grateloupia Desmoulini* of Lea (December, 1833), the former gave no figure, but Lea gave a good one¹ showing the hinge of the left valve, and this is certainly that of *Grateloupia*, as there are three prominent cardinal teeth, and several oblique ridges on the nymph. Whether the posterior cardinal is fused with the first of these ridges, or whether there is a groove between them, is of small importance, seeing that in *Tivela argentina* it is so fused, and in *T. radiata* it is not. There is therefore no essential difference between *G. hydana* and the other species of *Grateloupia*, and consequently there is no necessity to perpetuate the name of *Cytheriopsis* or its substitute *Grateloupina* (Dall).

CONCLUSIONS.

From the preceding notes and observations it will be seen that I regard *Tivela* as a fairly compact genus, including the fossils which have been described under the names of *Grateloupia* and *Cytheriopsis*. Consequently I consider that the genus ranges from the Eocene to the present day.

I have shown that the so-called accessory teeth are entirely confined to the nymphal plates, that they are merely ridges developed out of the rugose sculpture of these plates, and that the hinge of *Grateloupia* closely resembles that of some recent species of *Tivela*; also that *Cytheriopsis* does not seem to differ from *Grateloupia* in any essential respect.

¹ "Contributions to Geology," Philadelphia, 1833 (tract), pl. ii, fig. 33.

Further, I see no reason for retaining the *Pachydesma* of Conrad to include a few species which have a more vernicose periostracum than the rest, for the supposed existence of four cardinal teeth in these species is a mistake of Conrad's, repeated by Dall. The hinge of *Pachydesma* (i.e. *T. stultorum*) has been noticed on p. 267, and its dentition is merely one phase, among several, in the development of the nymphal ridges. It would be just as reasonable to separate those species which have two such ridges as to make a section out of those which have only one.

The only form, recent or fossil, which seems to have a character of subgeneric importance is *T. perplexa* (Stearns), in which the margins of the valves are crenulated, and for which Dall proposed the name of *Eutivela* in 1891.¹ I have referred to his description, which is accompanied by a woodcut of the left valve, and there can be no doubt that the shell is a *Tivela*. Judging from the figure the crenulations of the margin are distinct, though not in deep relief.

¹ *The Nautilus*, vol. v, p. 26.